

TRENDS IN ABUNDANCE OF NORTH ATLANTIC HUMPBACK WHALES IN THE GULF OF MAINE

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8

9 **Abstract**

10 The Gulf of Maine is the south-western most humpback whale feeding ground in the North
11 Atlantic Ocean, and the primary area in U.S. waters. This population has been the subject of
12 long-term photo-identification research since the late 1980s, but detailed studies of population
13 size and trend have been limited. We used annual surveys across the primary Gulf of Maine
14 feeding range and auxiliary data to estimate population size and growth from 2000 through 2016.
15 A Bayesian state-space open population model accounting for demography and individual
16 heterogeneity was implemented, and the results were compared to commonly used open-
17 population mark-recapture models and Minimum Number Alive enumeration methods. The best
18 estimate of 2016 abundance was 1,317 individuals (95% credible interval 1,278-1,350). Based
19 on ancillary data, we have evidence that the population was likely never below 701 individuals
20 during the study period, despite low abundances produced by the statistical models early in the
21 time series. The results further suggest that this is a mature population that has exhibited
22 relatively slow continued annual growth (geometric mean = 3.4%) since 2009. These findings

23 from long-term population research significantly improve understanding of a Federally-protected
24 species and its potential vulnerability to human impacts.

25

26 **Key-words:** Bayesian mark recapture, *Megaptera novaeangliae*, open population abundance,
27 population growth, recovery, survival

28

29 **Introduction**

30 Humpback whales are seasonal migrants with maternally-mediated site fidelity. The Gulf of
31 Maine, along the eastern boundary of the United States and Canada (Figure 1), is one of four
32 discrete humpback whale feeding grounds in the North Atlantic Ocean (Stevick et al. 2006).

33 This species feeds in the Gulf of Maine from March through December, but most individuals
34 migrate in winter to the West Indies where they calve and mate with whales from other North
35 Atlantic feeding grounds (Katona & Beard 1990).

36 Humpback whales were historically depleted by commercial whaling and were listed as
37 an Endangered Species in the U.S. for 45 years. Following a comprehensive status review
38 (Bettridge et al. 2015), the U.S. National Marine Fisheries Service (NMFS) recognized 14
39 distinct population segments (DPS) of humpback whales globally. The comprehensive status
40 review further determined that the West Indies DPS, including humpback whales that feed in the
41 Gulf of Maine, was not in need of protection under the Endangered Species Act¹. Nevertheless,
42 the specific details of population size and trend in the North Atlantic, including within U.S.

¹81 FR 62260, <https://www.gpo.gov/fdsys/pkg/FR-2016-09-08/pdf/2016-21276.pdf>

43 waters, were uncertain (Bettridge et al. 2015), and although the West Indies DPS is broadly
44 distributed across the North Atlantic in summer, local hazards and food resources may
45 potentially produce different fecundity and mortality schedules across feeding areas. A Federal
46 post-delisting monitoring plan was developed to address these data gaps and to detect adverse
47 effects following the status change (NMFS 2016).

48 In addition to functioning as important predators within a productive marine ecosystem,
49 humpback whales in the Gulf of Maine have been a key source of biological understanding of the
50 species and the focus of an economically important tourism trade. However, the Gulf of Maine
51 is an area of high human use and humpback whales feeding there have been subjected to a range
52 of unintentional anthropogenic impacts (van der Hoop et al. 2013; Henry et al. 2017). The U.S.
53 recognizes this humpback subpopulation as an important component of the Gulf of Maine
54 ecosystem and has produced regular assessments of its population status (e.g., Hayes et al. 2018).
55 Prior estimates of abundance for management purposes have been derived from line-transect
56 surveys and, more recently, enumeration metrics, but neither have provided adequate data on
57 population size or trends over time (Hayes et al. 2018). A recent study of North Atlantic right
58 whales applied a Bayesian state-space mark-recapture statistical model that both improved
59 population estimates and demonstrated a decline in abundance (Pace et al. 2017). We applied a
60 similar estimation approach and other mark-recapture approaches to a long-term photo-
61 identification data set to produce the first detailed time series of abundance and population
62 growth for Gulf of Maine humpback whales.

63

64 **Methods**

65 Humpback whales can be individually identified from their natural markings, particularly the
66 shape and ventral pigmentation pattern of the flukes (Katona & Whitehead 1981) and dorsal fin
67 characteristics (Katona & Whitehead 1981; Gill & Burton 1995; Blackmer et al. 2000). The
68 Center for Coastal Studies (CCS, Provincetown, MA, USA) has studied individual humpback
69 whales since the 1970s and maintains an extensive photo-identification catalog and life history
70 database of the Gulf of Maine humpback whale population. We used encounter histories of
71 individually-identified humpback whales from this long-term research to estimate population
72 abundance and growth from 2000 to 2016.

73 The primary data came from annual photo-identification surveys of Gulf of Maine
74 humpback whales across their primary feeding range from Nantucket, Massachusetts to Nova
75 Scotia, Canada (Figure 1). Humpback whales simultaneously occupy a wide range of coastal
76 and offshore areas within the Gulf of Maine and the Bay of Fundy during the summer, although
77 the specific distribution across these areas varies over time in relation to prey availability (Payne
78 et al. 1990; Weinrich et al. 1997). Vessel surveys therefore targeted as many of these humpback
79 whale aggregation sites as possible each year to increase the likelihood that any member of the
80 population had an opportunity to be sampled at least once. One notable exception was in 2011
81 when there was no coverage of the Canadian portion of the study area due to logistical issues.

82 Although this species can be encountered in the Gulf of Maine from March through
83 December, survey data analyzed for this study were limited to the peak of the feeding season
84 (June 22 through October 7). This period was selected because it excluded the shoulder seasons
85 when: 1) the population was likely open to demographically staged migration (Robbins 2007), 2)

86 transients from other feeding grounds were most likely to be present (Katona & Beard 1991) and
87 3) vessel survey effort was limited to the southwest Gulf of Maine.

88 For the purpose of mark-recapture statistical analyses, an individual was considered
89 “marked” in the year that fluke photo-documentation was adequate to ensure its uniqueness in
90 the population. Poorly documented animals were excluded from analysis because failure to
91 consider the quality of identifying documentation can result in false negative matches and
92 inflated abundance estimates (Friday et al. 2000; Stevick et al. 2001; Friday et al. 2008). In rare
93 cases (1%, n=23), an individual was known to have been alive in an earlier year based on lower
94 quality fluke documentation or secondary identification features. However, these earlier
95 sightings were excluded in the survey data set to avoid an inadvertent upward bias in survival
96 rates. We compressed all survey-based sightings of individual whales within a given year into a
97 binary annual outcome (seen or not seen). The resulting matrix of annual sightings became the
98 principal data used to estimate survival, recruitment, detection probabilities and hence
99 abundance.

100 In addition to survey-based mark-recapture data, we used auxiliary data to inform the
101 status of individuals, most notably for years prior to and after the study period. These data were
102 based on vessel surveys conducted by CCS from autumn through spring, but also included
103 information from a large network of opportunistic data contributors within the Gulf of Maine.
104 The latter were primarily formal data collection programs aboard whale watching vessels
105 operating coastally from Nantucket to Nova Scotia, but with a particular focus off the coast of
106 Massachusetts. All images submitted to and processed by CCS were considered for inclusion in

107 the auxiliary data set. As in the case of vessel survey data, we only included individuals once
108 they met the minimum photo-identification criteria of uniqueness in the population.

109 To further inform the modeling process we also used other information available from the
110 Gulf of Maine humpback whale catalog, including individual sex, known birth year or year of
111 first sighting and death year (if known). The sex of an individual was known from molecular
112 genetic analysis of a skin sample (Palsbøll et al. 1992; Bérubé & Palsbøll 1996a, b), observation
113 of the genital slit (Glockner 1983) and/or a calving history in the case of females. Exact age was
114 known for individuals that were first catalogued in their first year of life as dependent calves.
115 Individuals were considered juvenile until they reached age 5, which is the earliest age at first
116 calving although the average age is closer to nine years (Clapham 1992; Robbins 2007). Whales
117 that were first encountered after the calf year were at least one year old at the time of first
118 sighting, but could have been older. Prior research suggested that most, but not all, of the
119 individuals in this class were still juvenile (Robbins 2007). Individuals were categorized as dead
120 only if they were definitively matched to a carcass.

121 Most long-lived mammals exhibit variation in survival rates according to age and sex
122 (Caughley 1966). Age data, in particular, are rarely available for whale populations, but such
123 demographic trends have nevertheless been confirmed for well-studied populations (Fujiwara &
124 Caswell 2001; Ramp et al. 2010; Robbins et al. 2015; Pace et al. 2017), including this one
125 (Barlow & Clapham 1997; Robbins 2007). For statistical models, we discriminated five juvenile
126 age categories in light of previously documented age-specific survival rates: 0 (dependent calf), 1
127 (independent yearling), 2, 3 and 4 years. Animals known to be at least five years were grouped
128 into a single adult class (5+). Statistical models also treated animals of unknown age at entry as

129 age 5+. Although prior analyses suggested that they were likely younger than 5+ (Robbins
130 2007), their exact age was not known and a few may have been adults. Attempting to place these
131 individuals into discrete juvenile age classes was likely to inflate those survival rates and
132 artificially increase population size. We therefore took a precautionary approach and placed
133 them in the substantially larger adult sample, recognizing that doing so might depress estimates
134 of adult survival slightly (with a concomitant slight downward bias in abundance).

135

136 *Analytical methods*

137 We used several approaches to estimate the abundance and growth of humpback whales in the
138 Gulf of Maine in light of population characteristics and available data, as described below.

139

140 1) Minimum Number Alive

141 The Minimum Number Alive (MNA) can be calculated as the count of individuals known to be
142 alive in a year, because they were either seen in that year or seen both before and after that year
143 (Krebs 1966). This metric is likely to under-estimate true population size because it misses
144 animals that are alive but not yet cataloged, as well as cataloged animals that are still alive but
145 not re-sighted during the study period. It is also known to be particularly vulnerable to under-
146 estimation in the early and late portions of a data series (Hilborn et al. 1976; Efford 1992;
147 Pocock et al. 2004). Nevertheless, a reasonable estimate of minimum population size can be
148 useful in some management contexts, such as in the calculation of Potential Biological Removal
149 (Wade 1998). MNA has the potential to provide such information for Gulf of Maine humpback
150 whales because this species is long lived and because there has been considerable directed and

151 opportunistic effort to document individuals each year. Consequently, this simple accounting
152 procedure has informed resource management in the past (e.g., Waring et al. 2015; Waring et al.
153 2016).

154 We calculated three MNA metrics annually from 2000 through 2016 to compare to mark-
155 recapture statistical abundance estimates. *MNA-Survey* was based exclusively on the dedicated
156 survey encounter data. *MNA-Survey+* included only individuals seen at least once in the
157 dedicated survey but used all available information to determine their status in a given year.
158 *MNA-All* was calculated using all available sightings of Gulf of Maine humpback whales.
159 Calves were included even if they were not adequately marked because they were known to be
160 individuals by association with their uniquely marked mother, even if they could not be reliably
161 recognized in subsequent years. When auxiliary data were added to the survey data, they
162 included re-sightings through 2017 to minimize, but not eliminate, bias in the last interval.
163 These simple enumerations of minimum population size were plotted against statistical estimates
164 of abundance. We also calculated the age and sex composition of the largest MNA estimates for
165 comparison to survey data.

166

167 2) Jolly-Seber open-population mark-recapture model

168 We used open population mark-recapture models to estimate abundance in light of the fact that
169 individuals were not seen in all years and did not necessarily survive from one sampling period
170 to the next. As an initial approach, we first calculated abundance using a Jolly-Seber (J-S) model
171 (Jolly 1965; Seber 1965) without accounting for age, sex or individual heterogeneity.

172 Calculations were performed using Program R (R Development Core Team 2012) package

173 “Recapture” (Rivest & Baillargeon 2014) under both unrestricted capture rates and time invariant
174 capture rates. Open-population mark-recapture models make assumptions of capture and
175 survival probability homogeneity among individuals, which is often extended to groups in more
176 complex models (Williams et al. 2002). However, as noted previously, prior mark-recapture
177 studies of this population have shown that survival varies by age and sex, that effort and success
178 of re-sighting whales varies over time and that capture probabilities are heterogeneous across
179 individuals (Robbins 2007; Ford et al. 2012). It is rarely the case that both sex and age data are
180 systematically available for whale populations and the most recent prior estimates for both the
181 Gulf of Maine and the North Atlantic have not used such data (Clapham et al. 2003; Stevick et al.
182 2003). We were therefore interested to determine how simple J-S approaches omitting likely
183 important group heterogeneity in survival and capture processes would compare to MNA as well
184 as more robust estimation techniques.

185

186 3) Bayesian state-space models

187 We implemented a mark-recapture statistical modeling approach similar to one recently
188 employed to assess population abundance trends in North Atlantic right whales (Pace et al.
189 2017). Re-sighting histories of known individuals were used to estimate survival rates and
190 abundance in a Bayesian, state-space formulation estimated using Markov Chain Monte Carlo
191 (MCMC) simulation. Specifically, we modified the approaches of Kéry and Schaub (2011) and
192 Royle and Dorazio (2012) to produce a multi-state formulation which relied on J-S model ideas
193 of estimating the probability of new member entry but executed it in a Bayesian framework
194 together with data augmentation. We separated the likelihoods associated with state transition or

195 biological process from that of the observation process. The biological states modeled were: 1)
196 not yet entered into the population, 2) alive and 3) dead. The 2 observed states were seen or not
197 seen. All other values in the state matrix were coded as unknown (NA). States were also
198 informed by auxiliary information. For example, an animal known to have been alive in 1995 but
199 was not seen in the survey until 2002, it was coded as alive in 2000 and 2001. If an animal was
200 of unknown age when first seen in the survey, its states in the data matrix prior to the year first
201 seen were treated as unknown. To estimate probability of entry in the population, which is a
202 necessary parameter for the derivation of abundance estimates, we augmented the capture
203 histories with 300 histories that represent animals never seen, but that could enter the population
204 and still never be seen based on estimated capture, survival and entry probabilities (Royle &
205 Dorazio 2012).

206 We used logistic relationships with linear combinations of predictors (Lebreton et al.
207 1992) to estimate survival and capture probabilities while accounting for sources of
208 heterogeneity. In the main model, survival probability was modeled as:

$$209 \quad \text{Logit}(\phi_{i,t}) = \beta_1 + \beta_2 * (1 - \text{sex}_i) * \text{Adult}_{i,t} + \beta[\text{Age}_{i,t}] + \epsilon_t$$

210 Where: $\phi_{i,t}$ is survival probability of the i^{th} individual for the t^{th} interval, β_1 is the intercept
211 whose value in the logit is the mean of calf survival, β_2 is the added effect of being a female > 4
212 years old on survival, sex_i is a data value of 0 for female, 1 for male and NA for unknown,
213 $\text{Adult}_{i,t}$ is a data value of 1 if the i^{th} animal is classed as age > 4 in the t^{th} interval, $\beta[\text{Age}_{i,t}]$ is a
214 set of factors for each age group 1,2,3, 4 and 5, $\text{Age}_{i,t}$ is an index representing an age value
215 ranging from 1 – 5 for the i^{th} individual at time interval t , and ϵ_t is the random effect of year on
216 survival.

217 Similarly, we modeled capture probability as:

$$218 \quad \text{Logit}(P_{i,t}) = \alpha_1 + \alpha_2 * (\text{sex}_i) + \alpha_3 * (1 - \text{Adult}_{i,t}) + \text{Time}_t + \zeta_i$$

219 Where: α_1 was the intercept and hence the effect of being a female on capture probability, α_2 was
220 the added effect of being a male on capture probability, α_3 was the added effect of being a
221 juvenile on capture probability, Time_t was the linear effect of the year t on average capture
222 probability with $\text{Time}_t=2000$ was 0, and ζ_i was the random effect of the i^{th} individual on capture
223 probability.

224 For estimation, we assigned vague priors on all linear logistic terms except the random
225 coefficients ε_t and ζ_i , as $\text{uniform}(-10,10)$. Random coefficients ε_t and ζ_i were given normal $(0, \delta)$
226 and normal $(0, \sigma)$ priors, respectively. Standard deviation terms δ and σ were given vague priors
227 of $\text{uniform}(0.001,10)$. The probability of entry into the population, γ_t , was allowed to vary
228 among time intervals, and each γ_t was assigned a $\text{uniform}(0,1)$ prior. Transitions among states
229 (not yet entered, alive or dead) were modeled as a discrete categorical random variable
230 dependent on the prior state according to the following probabilities:

231

State	Not entered	Alive	Dead
Not entered	$1 - \gamma_t$	γ_t	0
alive	0	$\phi_{i,t}$	$1 - \phi_{i,t}$
dead	0	0	1

232

233 The observed data (seen or not seen) were considered dependent on the animal's state and were
234 modeled as Bernoulli($p[s]$) according to the following:

State	Seen	Not Seen
Not entered	0	1
Alive	$P_{i,t}$	$1-P_{i,t}$
Dead	0	1

235

236 Finally, missing data on the sex of individual whales was modeled as Bernoulli(ρ), where ρ was
237 given a somewhat informative beta(5,5). Using the above structure, data were modeled using
238 program JAGS (Version 4.0.0) MCMC simulator (Plummer 2003) accessed via Program R (R
239 Core Team 2012) and package “run.jags” (Version 2.0.2-8, Denwood 2016). When dealing with
240 model parameters in all simulation exercises, we provided random starting values from within
241 the range of the prior for that parameter. Covariates concomitant with capture histories in the
242 data augmentation set were unknown for sex and age=5 and adult=1 adult for age class.
243 We provided initial values for unknown states ($state.init_{ij}$) which were $state.init_{ij}=1$ prior to the
244 first year seen and $state.init_{ij}=3$ after the last year seen, and a value of 1 for all animals in the
245 augmentation set of capture histories. Unknown sexes were assigned a Bernoulli(0.5) random
246 initial value. We used an adaptation + burn in phase of 5,000 iterations and sample size of
247 20,000 iterations for estimation. JAGS code for the primary model is provided in Appendix I. In
248 all cases, to determine when the algorithms had converged, we used three chains and computed
249 the Gelman-Rubin convergence statistic, which we required to be <1.1 for all model parameters
250 (Gelman & Rubin 1992).

251 In addition to the primary model defined above, we fit 3 other models of covariate
252 structure to these data:

- 253 1. Time as a fixed factor deterministic covariate to predict survival with all other structure
254 unchanged from the primary model;
- 255 2. Age as a fixed factor covariate to predict survival with all other structure unchanged from
256 the primary model; and
- 257 3. The random factor ζ_i deleted from the estimation of capture probability with all other
258 structure unchanged from the primary model.

259

260 *Population growth rate*

261 Population growth was estimated from the Bayesian state-space model as described by Pace et
262 al. (2017). Specifically, it was calculated for each time step as N_{t+1}/N_t , where the values
263 selected for N_t were the median values among the MCMC chains.

264

265 **Results**

266 Analyses were based on capture histories of 1,612 individuals identified during population
267 surveys. The sample included 608 females, 648 males and 356 animals of unknown sex. A total
268 of 544 animals had been identified and cataloged prior to the start of the study in 2000 and 601
269 individuals were known to have been born during the study period. The remaining 467 animals
270 entered the study after 1999 at an unknown time after birth.

271 The whales identified through surveys represented 71.6% of the 2,252 adequately marked
272 individuals detected alive at least once by any source during the same span of years. The vast
273 majority of the whales that were missed by surveys were only seen by other sources in one or
274 two years (89.5%, $n=573$). The 24 individuals that were seen outside of survey effort in four

275 years or more were predominantly present in the shoulder seasons, but not exclusively. Only
276 1.6% (n=37) of catalogued individuals were known to have died during the study period,
277 although this under-estimates mortality because not all deaths were necessarily documented or
278 individually-identifiable due to decomposition. Females were slightly favored in each annual
279 survey sample (1.09:1). As shown in Figure 2, the majority of each annual survey sample was
280 mature (mean=70.7%) and ranged from 57.4% (2009 and 2010) to 85.6% (2013).

281

282 *Minimum Number Alive*

283 Each calculation of Minimum Number Alive in the Gulf of Maine increased the more auxiliary
284 observations were included, such that $MNA-All > MNA-Survey+ > MNA-Survey$ (Table 1; Figure
285 3). All annual estimates also continued to increase as more time was allowed to elapse from the
286 base year. Thus, the greatest change was for 2000, which increased by 43.8% (n=295, *MNA-All*)
287 between the base year and 2017. For all MNA estimates, the largest count was in the middle of
288 the study period, preceded by an upward trend in the early series and followed by a downward
289 trend in the later series (Figure 3). Based on the most inclusive estimate (*MNA-All*), the
290 population was never below its starting minimum abundance of 701 individuals in 2000.
291 Furthermore, the highest MNA estimate suggests that there were no fewer than 1,021 individuals

292 alive in 2009. Like the survey data, mature whales dominated each annual sample (Figure 2),
293 ranging from 60.8% (2009) to 83.7% (2013).

294

295 *Abundance models*

296 The simple J-S model produced abundance estimates that mirrored the temporal trends of MNA
297 series estimates (Figure 3). Specifically, they suggested increasing abundance in the early
298 portion of the study, with a peak in 2009 followed by population decline. The J-S estimates also
299 tended to be biased low, with 95% confidence intervals often falling below MNA estimates
300 (Figure 3). This pattern was most notable in the early and late periods when even MNA
301 estimates are expected to be biased downward. This naïve model also suggested relatively low
302 and imprecise survival rates with overlapping confidence intervals for most years (Figure 4), at
303 least in part a likely consequence of a failure to account for group heterogeneity in survival.

304 The primary multi-state Bayesian mark-recapture model employed here had excellent
305 convergence statistics as judged by the computed Gelman-Rubin convergence statistics
306 (Appendix I) and posterior distributions for all linear (logistic) parameters associated with time.
307 Sex and age covariates contributed significantly (i.e., were distinct from zero) to estimates of
308 survival and capture probability (Appendix I). Adults had significantly higher survival rates that
309 were also more precise and less temporally variable than calf survival (Figure 5).

310 Abundance estimates from the state-space model ranged from 286 (95% credibility
311 interval 250-325) in 2000 to 1,317 (95% credibility interval 1,278-1,350) in 2016 (Figure 6).
312 These estimates were considerably more precise than those generated by the simple J-S mark-
313 recapture model and exceeded the lowest MNA counts (*MNA-Survey*) in all years. They also met

314 or exceeded the more inclusive lower population bounds, *MNA-Survey+* and *MNA-All*, from
315 2006 onwards (Table 1). However, the early estimates (2000-2002, in particular) were lower
316 than the minimum number of whales known to be alive in the population and the cause of these
317 under-estimates is unclear. State-space model estimates suggested a pattern of increase across
318 most of the study period, with the exception of 2004-2006 and 2011-2013. Both of these periods
319 involved years of lower apparent calf survival (Figure 5) and ended with the lowest annually
320 estimated fraction of juveniles (2006 and 2013-14, Figure 2). However, abundance and survival
321 were predicted to have increased at the end of the study period when both MNA metrics and
322 simple J-S models indicated population decline (Figure 3).

323 By estimating the unknown sexes as part of the model, we were able to separately
324 estimate male and female abundance (Figure 7). Male abundance was consistently greater than
325 female abundance and this difference increased over time. The model included a parameter to
326 account possible differences in survival between male and female adults and these estimates
327 indicated that females survived at a lower rate.

328

329 *Population growth rate*

330 Annual population growth was estimated to be positive in all but three years of the study (2011-
331 2013, Figure 8). However, estimates for the first three years exceeded biologically plausible
332 rates for *in situ* growth in this species (11.8%, Zerbini et al. 2010) and corresponded to a
333 sequence of abundance estimates that considerably under-performed relative to MNA.
334 Excluding those initial values, the geometric mean population growth from 2004-2016 was 1.05.
335 This mean was largely driven by three years of peak growth ending in 2008, two years of which

336 also slightly exceeded plausible growth rates. Since 2009, the geometric mean population growth
337 rate has averaged 1.03.

338

339 **Discussion**

340 This study provides the longest and most precise time series of abundance for humpback whales
341 that feed in the Gulf of Maine. It was based on 17 years of directed vessel survey effort spanning
342 the primary feeding range, and informed by 40 years of long-term population monitoring and
343 data from a large, opportunistic data collection network. This research also utilized sophisticated
344 mark-recapture statistical approaches to specifically account for potential sources of
345 heterogeneity and to provide the best information in light of uncertainty. The results suggest a
346 mature population that has likely nearly doubled in the past decade and continues to exhibit
347 relatively slow growth in recent years. These findings significantly improve understanding of a
348 Federally-protected species and its potential vulnerability to human impacts.

349 Three methodological approaches were used to estimate abundance from photo-
350 identification data. The Bayesian state space mark-recapture model was similar to the approach
351 recently used to better understand the abundance and trend of the endangered North Atlantic
352 right whale (Pace et al. 2017). Here, our model provided the most precise estimates that were
353 also the most plausible for the second half of the study period. By contrast, a simple J-S model
354 failing to account for age, sex and heterogeneity often failed to match even the minimum known
355 number of whales known to be alive in the population. Simple models are often used in whale
356 research because detailed data on individuals is often lacking. Prior studies on humpbacks and
357 other species in the Gulf of Maine indicate the importance of accounting for sex, age and

358 heterogeneity (Hammond 1990; Robbins 2007; Ford et al. 2012; Robbins et al. 2015; Pace et al.
359 2017), and our results suggest significant loss in precision and potentially bias in simple open
360 population estimates. An important consideration for those that might consider mark-recapture
361 estimates of abundance for humpbacks on a feeding ground is the apparent importance of
362 individual variability in capture probability. In this study, consider that the parameter as
363 displayed in the state-space model is an additive term in a logit model, and its influence on
364 individual capture probability varies depending on the group mean proximity to 0.5. The
365 posterior distribution of the median standard deviation of the random effect of individual
366 catchability (in the logistic) was 1.238 (95% credible interval: 1.176-1.300). Based on the
367 median estimate and a group mean of at 30% capture probability, catchability among 95% of the
368 individuals in that group could range from 0.05 to 0.76. Such a large range suggests likely
369 violation of assumptions of group capture homogeneity in any simple mark-recapture model.

370 The Minimum Number Alive has previously informed the management of this
371 population, as it is a precise minimum of population size required for calculations of Potential
372 Biological Removal (Wade 1998). While true population size cannot be lower than the MNA, it
373 may be substantially higher. In this study, there was considerable effort to detect humpback
374 whales opportunistically, as well as through dedicated surveys, and so MNA provided a valuable
375 baseline for understanding the performance of the statistical models. It provided particular
376 insight into minimum abundance in the early years of the study, which were under-estimated by
377 both the Bayesian state space and the simple J-S models. The use of three forms of MNA also
378 demonstrated how inference improves with the inclusion of more data. However, MNA is not a
379 reliable metric for time-sensitive population monitoring or for population trend because it relies

380 upon sampling effort in prior and subsequent years to counter the incomplete detection
381 probabilities of individuals. In our study, annual counts continued to increase across the study
382 period, by as much as 43%, based on detections made after the base year. Yet, even after many
383 years, these counts were likely incomplete to an unknown degree and also biased in that
384 individuals and groups with lower survival rates are less likely to ever be accounted for. The
385 downward bias in the second half of the series is a known issue with this population metric
386 (Pocock et al. 2004), and worsens with long-lived animals and low capture probabilities.

387 The Bayesian state-space model estimate for 2011 (N=1,175 95% credibility interval
388 1,143-1,206) was substantially higher and more precise than the line-transect estimate most
389 recently used for population management (N=335, CV=0.42, 2011, Hayes et al. 2018). Our
390 results also update the last used MNA estimate (Hayes et al. 2018), derived earlier from this
391 research, from 823 to 969 in 2008. The most recent abundance estimate for the Gulf of Maine
392 using mark-recapture statistical techniques was based on the YONAH project in 1992-1993 and
393 indicated an abundance of 652 (CV=0.29) (Clapham et al. 2003). That published estimate
394 approaches the lowest possible size of the population at the start of this study seven years later
395 (701, *MNA-All*). Our statistical models unfortunately provide limited insight into true abundance
396 at the start of the study period. However, available data suggests that there may have been
397 relatively little net population growth in the preceding decade. The Clapham et al. (2003) study
398 estimated the population growth rate as 1.00 (for a calf survival rate of 0.51) or 1.04 (assuming
399 0.875), and the lower of the two calf survival rates was later determined to be more plausible for
400 the study period Robbins (2007). Both estimates were significantly lower than the mean
401 population growth rate estimated for the years 1979 through 1991 (1.065, Clapham et al. 2003),

402 during which time the overall West Indies DPS was thought to be growing more slowly (3.1%,
403 1979-1993, Stevick et al. 2003).

404 Our results suggest that the population was growing throughout most of the study period,
405 albeit relatively slowly in most years. This is consistent with the relatively small juvenile
406 component detected in the population throughout the study. However, there appear to have been
407 two periods of slower growth or decline, the first around 2006 and the second from 2011-2013.
408 Model-based estimates of population growth rate, abundance estimates and calf survival are
409 inter-related but these periods correspond to years with the lowest frequency of juveniles of the
410 population. Nevertheless, the cause of these potential demographic events is not clear. There
411 have been three Unusual Mortality Events (UME)² involving humpback whales during the period
412 of this study. The first two (in 2003 and 2005) occurred during a period in which our model-
413 based estimates are least informative. The latest and largest UME is on-going since 2016, and
414 any effects would not yet be reflected in these estimates. In the latter case, the majority of
415 detected carcasses have thus far been found south of the Gulf of Maine. Continued population
416 research may help to determine the degree of impact on humpback whales in the Gulf of Maine.

417 Our results are notable in relation to a comparable study recently conducted on North
418 Atlantic right whales (Pace et al. 2017). The finding of lower survival and abundance of adult
419 females in that study was also found here, where it was consistent with previous evidence of sex-
420 stratified adult survival in this population (Robbins 2007). The latter research found that

² <https://www.fisheries.noaa.gov/national/marine-life-distress/2016-2018-humpback-whale-unusual-mortality-event-along-atlantic-coast>

421 survival among adult female humpback whales in the Gulf of Maine was specifically lower in
422 the interval after calving, suggesting a cost of reproduction. The only other sex-stratified
423 survival estimate for this species comes from another North Atlantic population in the Gulf of St.
424 Lawrence, Canada in which male survival was found to be lower than female survival (Ramp et
425 al. 2010). However, females in that study area also have a lower average calving interval than
426 females in the Gulf of Maine (Ramp 2008). This cautions against assuming species-level
427 patterns in survival or fecundity principles from a single population, or extrapolating vital rates
428 to populations with potentially different ecological conditions and hazards.

429 Overall, our results suggest a mature population that is still growing following its status
430 change under the Endangered Species Act, and despite well-documented human impacts. They
431 highlight the value of long-term humpback whale population research for effective management
432 and conservation.

433

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441 Gulf of Maine Humpback Whale Catalog: 7 Seas Whale Watch, Blue Ocean Society, Bar Harbor
442 Whale Watch, Boston Harbor Cruises, Brier Island Whale and Seabird Cruises, Cape Ann Whale

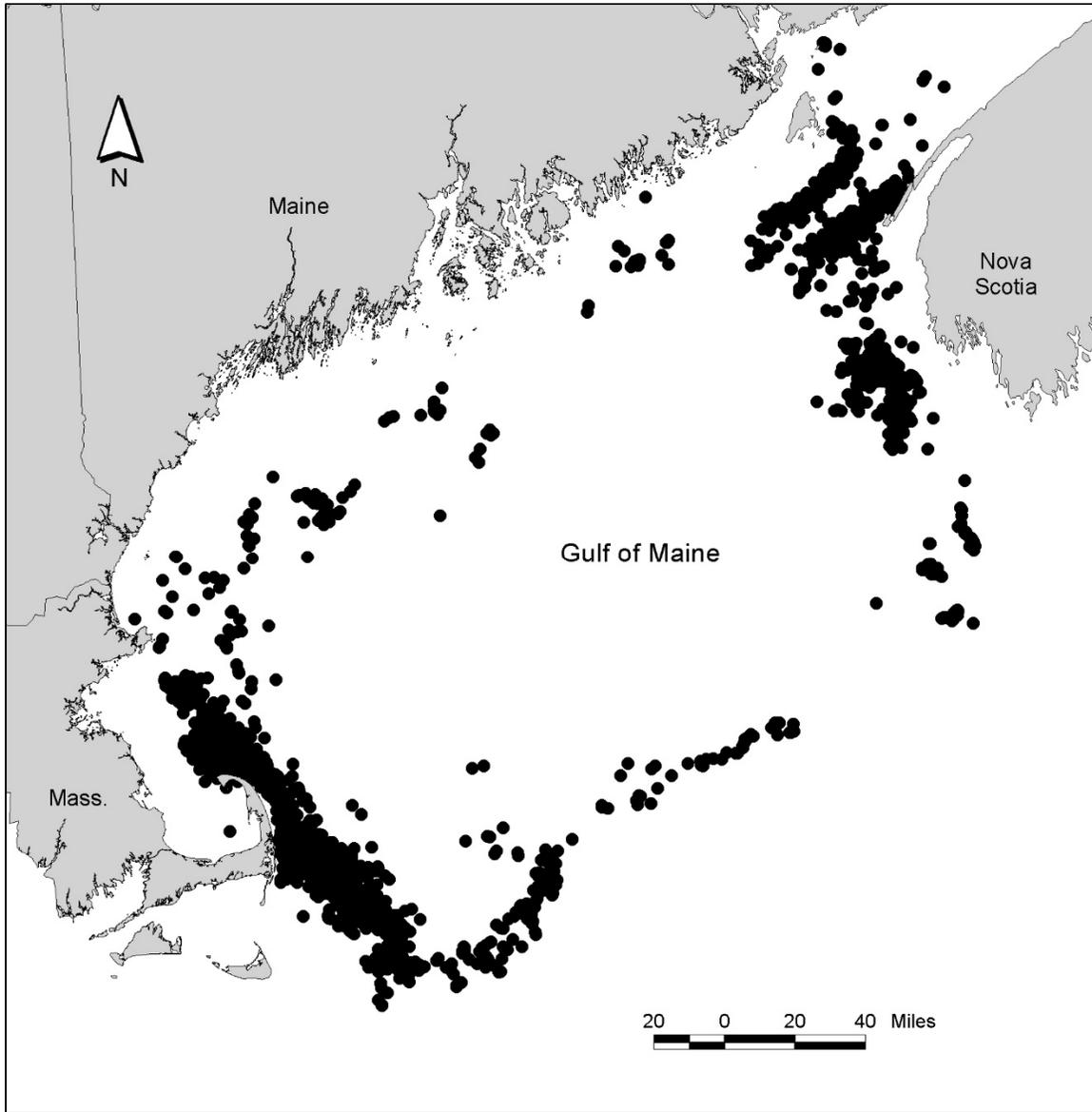
443 Watch, Coastal Research and Education Society of Long Island, Dolphin Fleet Whale Watch,
444 Grand Manan Whale and Seabird Research Station, Hyannis Whale Watcher Cruises, New
445 England Aquarium, New England Coastal Wildlife Alliance, Newburyport Whale Watch,
446 Quoddy Link Marine, Whale and Dolphin Conservation, the Whale Center of New England and
447 others. The Northeast and Southeast Marine Mammal Stranding Networks provided photographs
448 used to identify catalogued whales after death. Analyses were supported by the NMFS Northeast
449 Fisheries Science Center (EE133F-17-SE-1320).
450

451 Table 1. Point estimates of abundance derived using 3 accounting procedures and 2 statistical
 452 mark recapture models for individually identifiable Gulf of Maine humpback whales observed
 453 during 2000-2016.

Year	<i>MNA-Survey</i>	<i>MNA-Survey+</i>	<i>MNA-All</i>	Simple J-S	J-S State Space
2000	171	573	701	-	286
2001	233	583	701	438	385
2002	338	641	805	601	516
2003	507	705	822	663	681
2004	516	708	828	813	747
2005	553	715	810	706	772
2006	551	694	784	672	783
2007	621	750	868	795	889
2008	698	830	969	922	1015
2009	698	853	1021	966	1126
2010	721	885	1016	923	1196
2011	625	800	939	822	1175
2012	608	769	899	737	1168
2013	570	749	829	699	1126
2014	562	751	859	776	1181
2015	601	779	942	720	1281
2016	345	572	808	-	1317

454

455 Figure 1: Humpback whale sightings from annual vessel surveys in the Gulf of Maine, 2000-
456 2016. Black circles represent the first sighting per identified individual per year, June 22
457 through October 7.
458

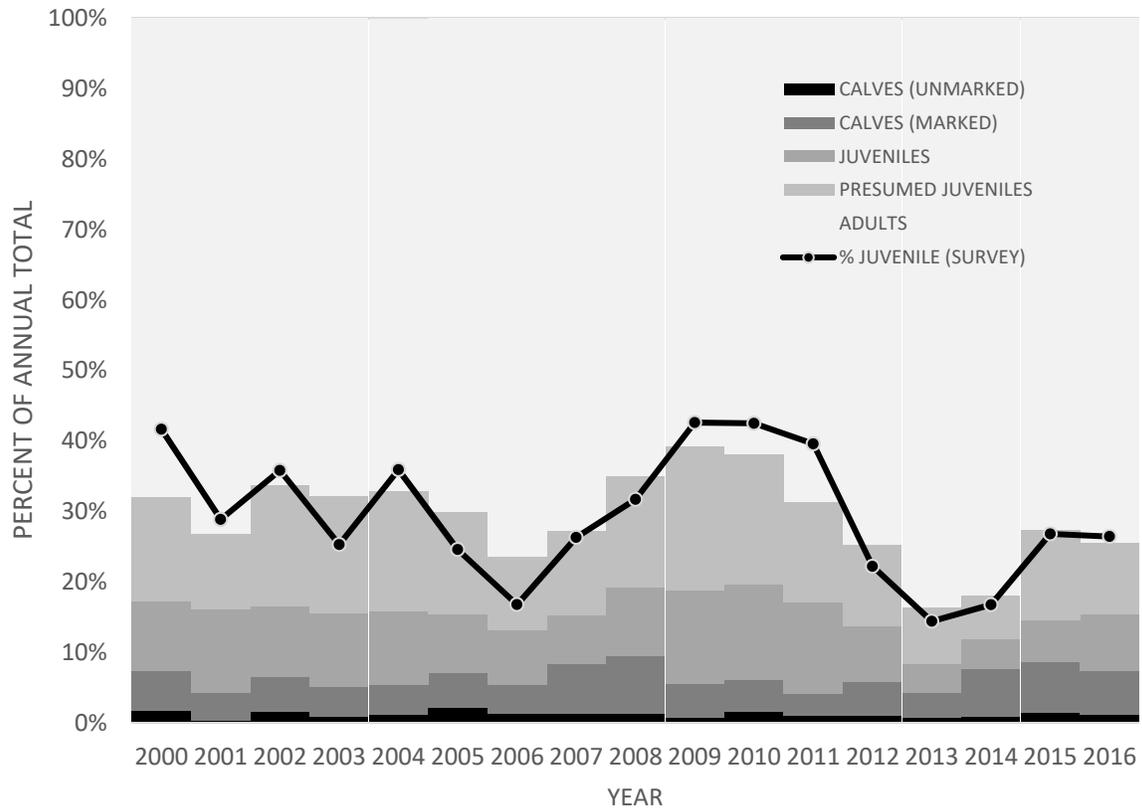


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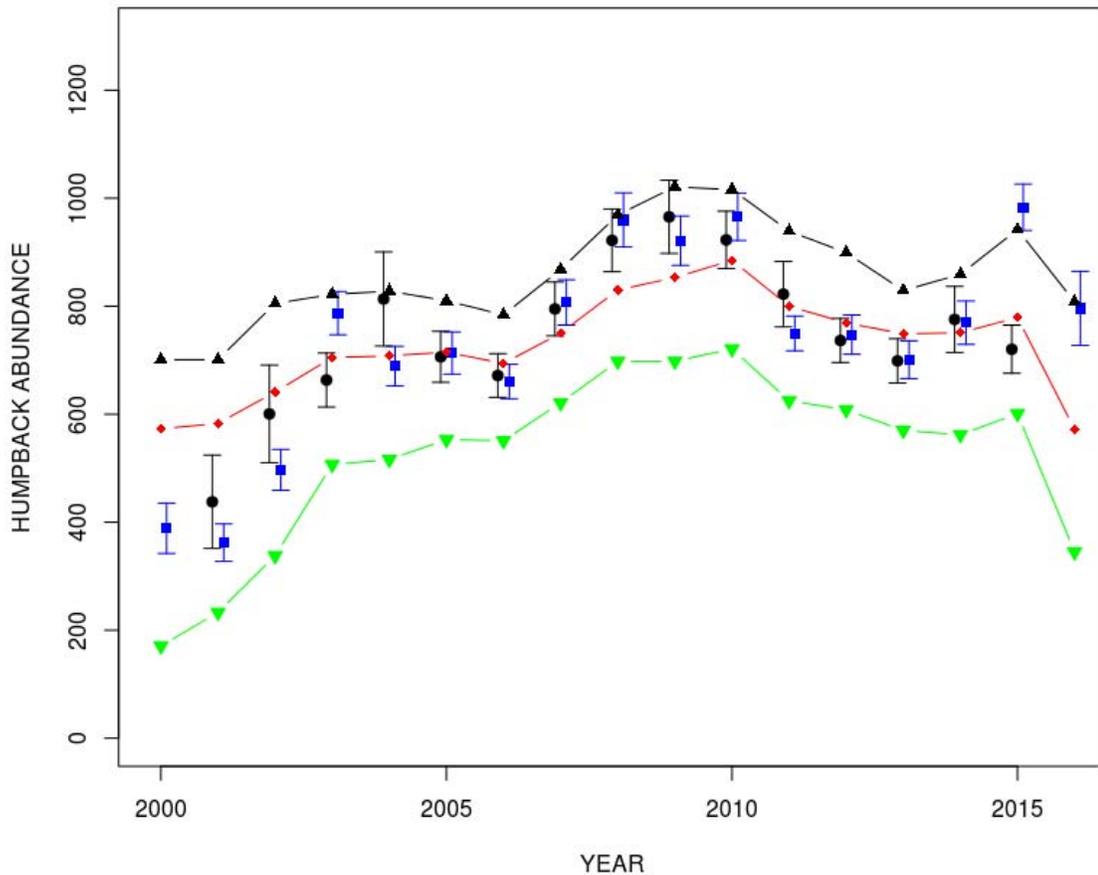
461 Figure 2: Annual age class composition of the *MNA-All* sample (stacked bars) and the
 462 percentage of known and suspected juveniles in the survey data (line).

463



464

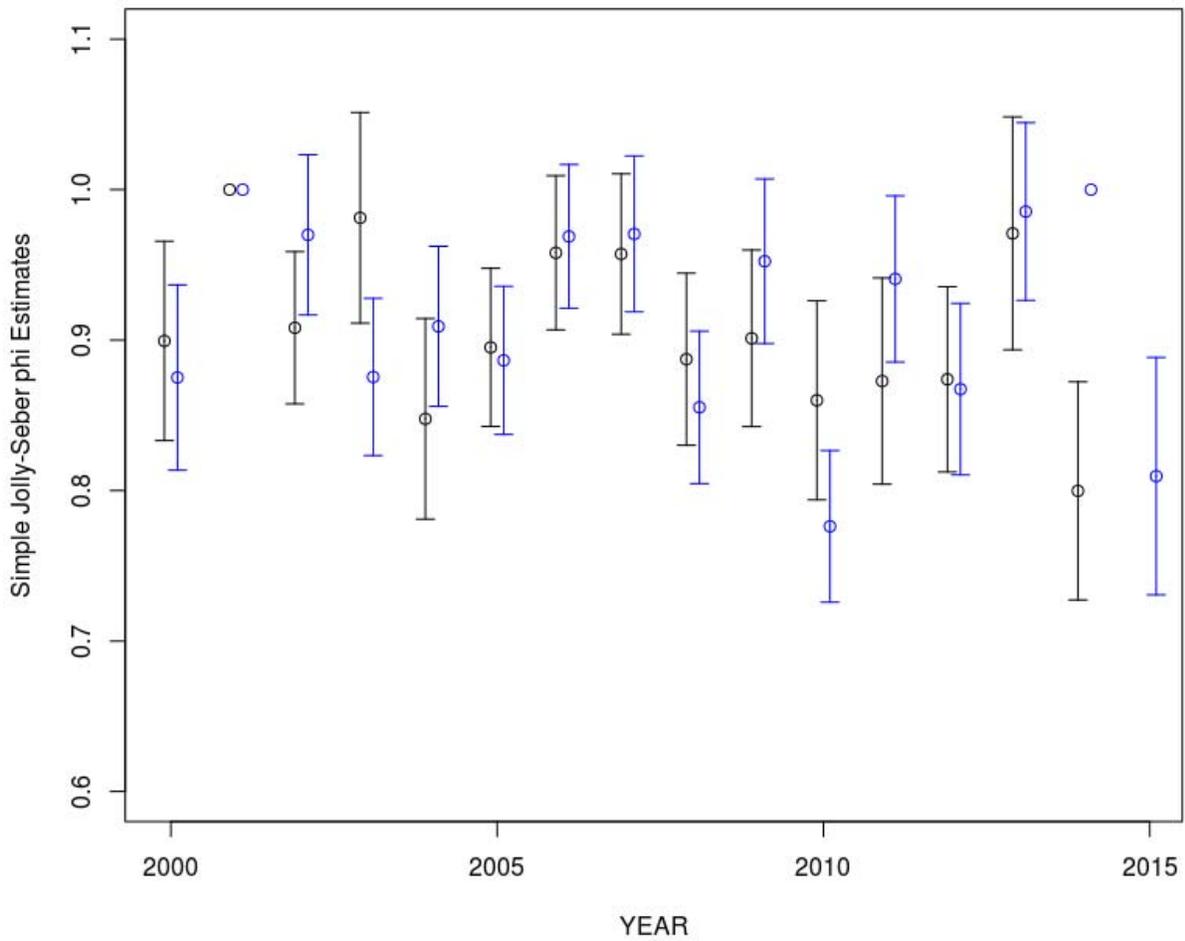
465 Figure 3: Jolly-Seber abundance estimates for 2000-2016, assuming capture probabilities as
466 time-varying (black squares) or constant (blue squares). Error bars represent the 95%
467 confidence interval. Also depicted are Minimum Number Alive metrics: *MNA-All* (black
468 triangles), *MNA-Survey+* (red diamonds) and *MNA-Survey* (green triangles).



469

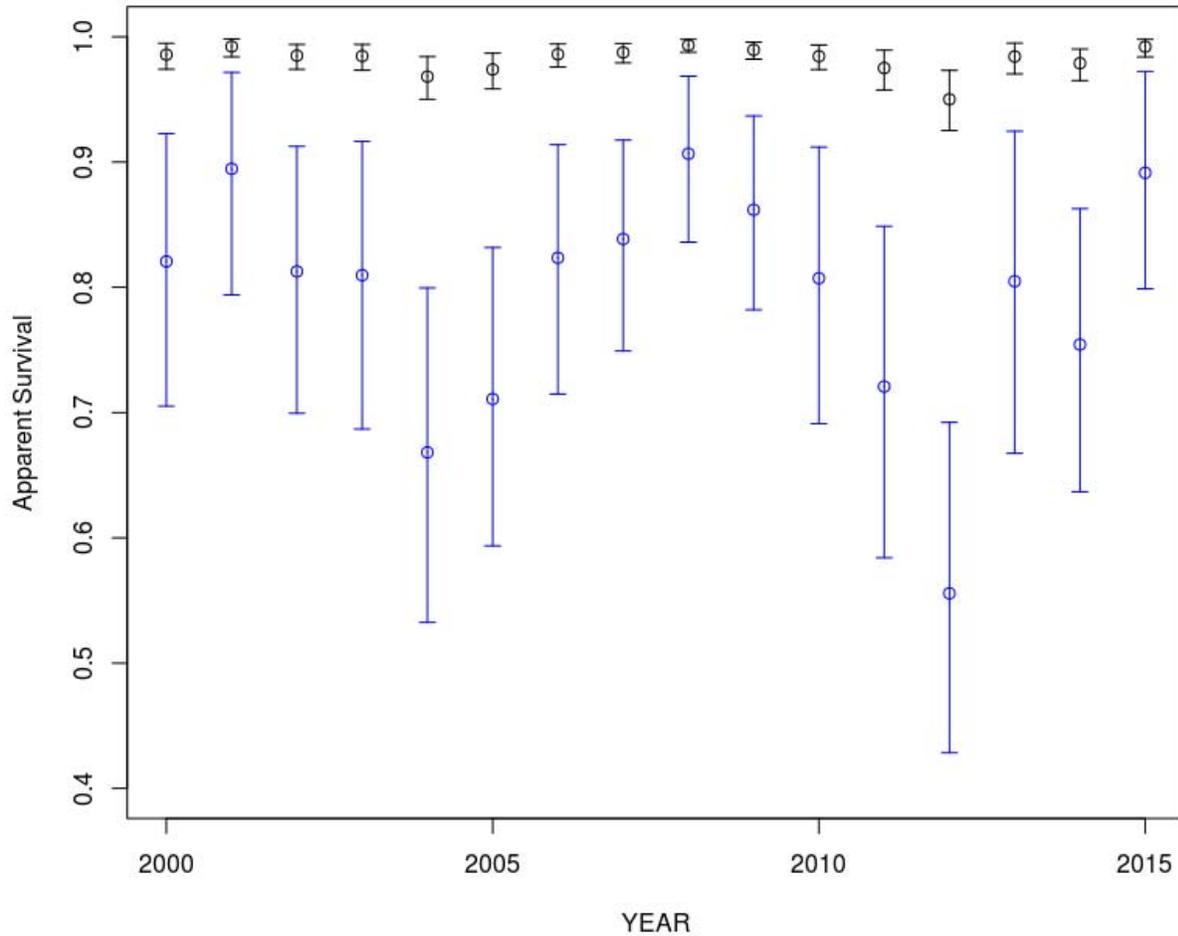
470

471 Figure 4: Survival estimates for 2000-2016, generated from the Jolly-Seber mark-recapture
472 model. The model assumed capture probabilities as time-varying (open black circles) or constant
473 (open blue circles). Error bars represent the 95% confidence interval.



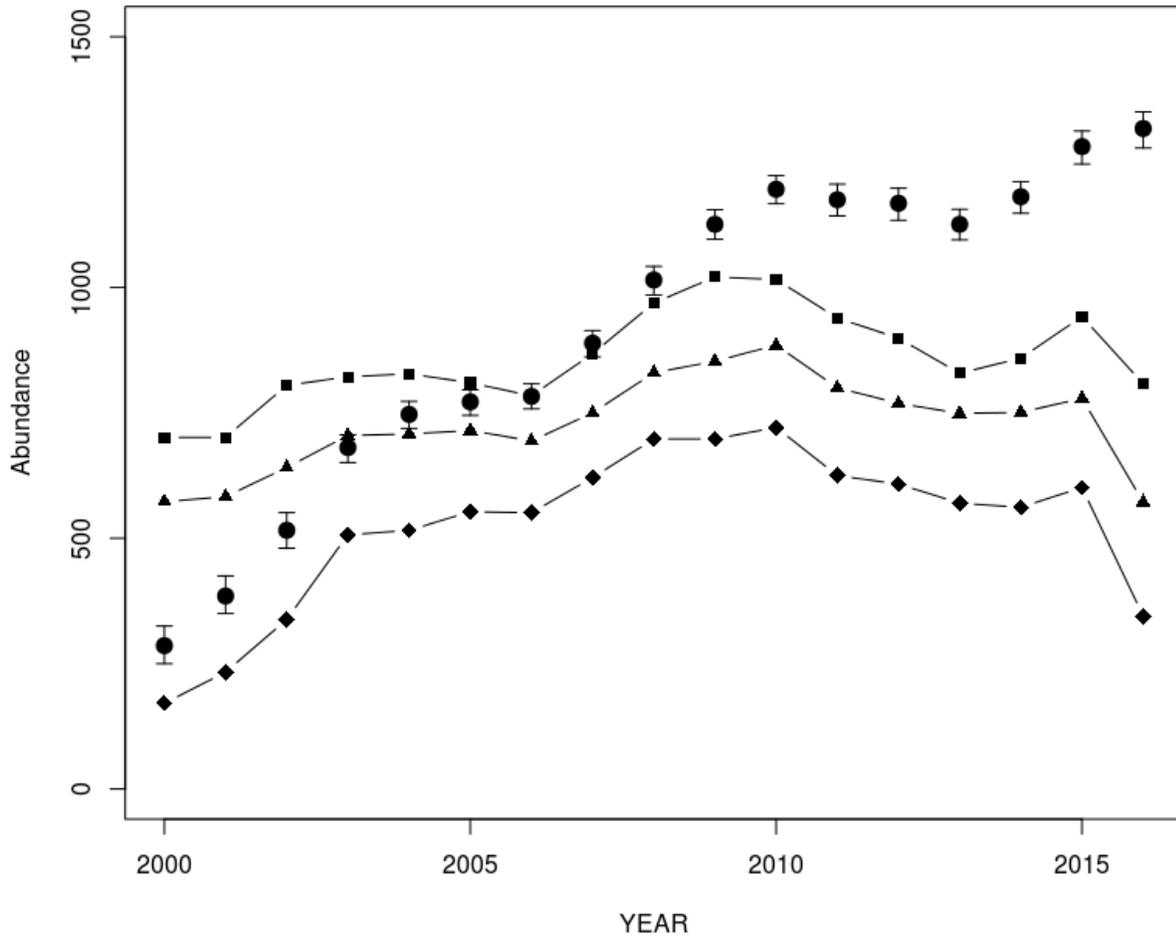
474

475 Figure 5: Apparent survival of adult females (black circles) and calves of both sexes (blue
476 circles) in the Gulf of Maine from 2000 through 2016. Error bars are posterior medians from a
477 Bayesian mark-recapture model allowing random fluctuation among years, age effects and adult
478 female effects on survival, as well as sex and time effects and random effects of individual
479 catchability on capture probabilities together with their 95% critical regions



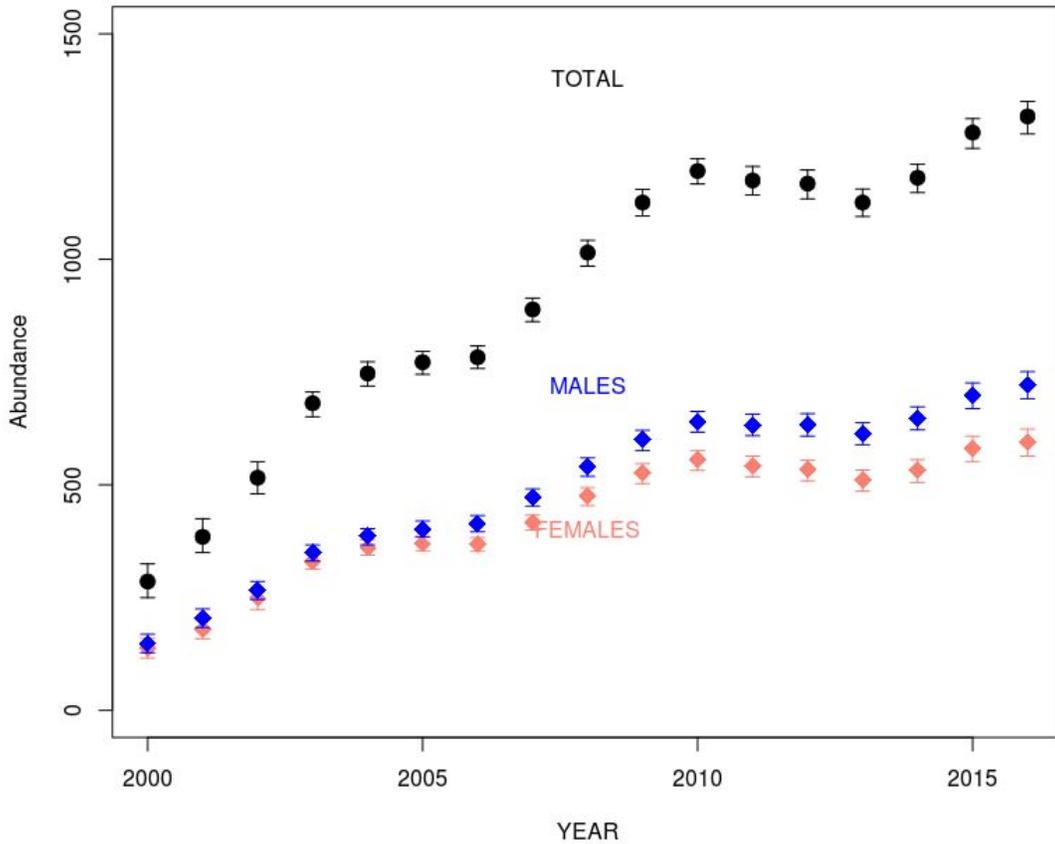
480

481 Figure 6: Annual abundance of Gulf of Maine humpback whales calculated by four procedures.
 482 Solid circles with error bars are posterior medians from a Bayesian mark recapture model
 483 allowing random fluctuation among years, age effects and adult female effects on
 484 survival, as well as sex and time effects and random effects of individual catchability on
 485 capture probabilities together with their 95% critical regions. Minimum number alive
 486 (MNA) estimates are dashed lines with diamonds (*MNA-Study*), triangles (*MNA-Study+*)
 487 and squares (*MNA-All*).



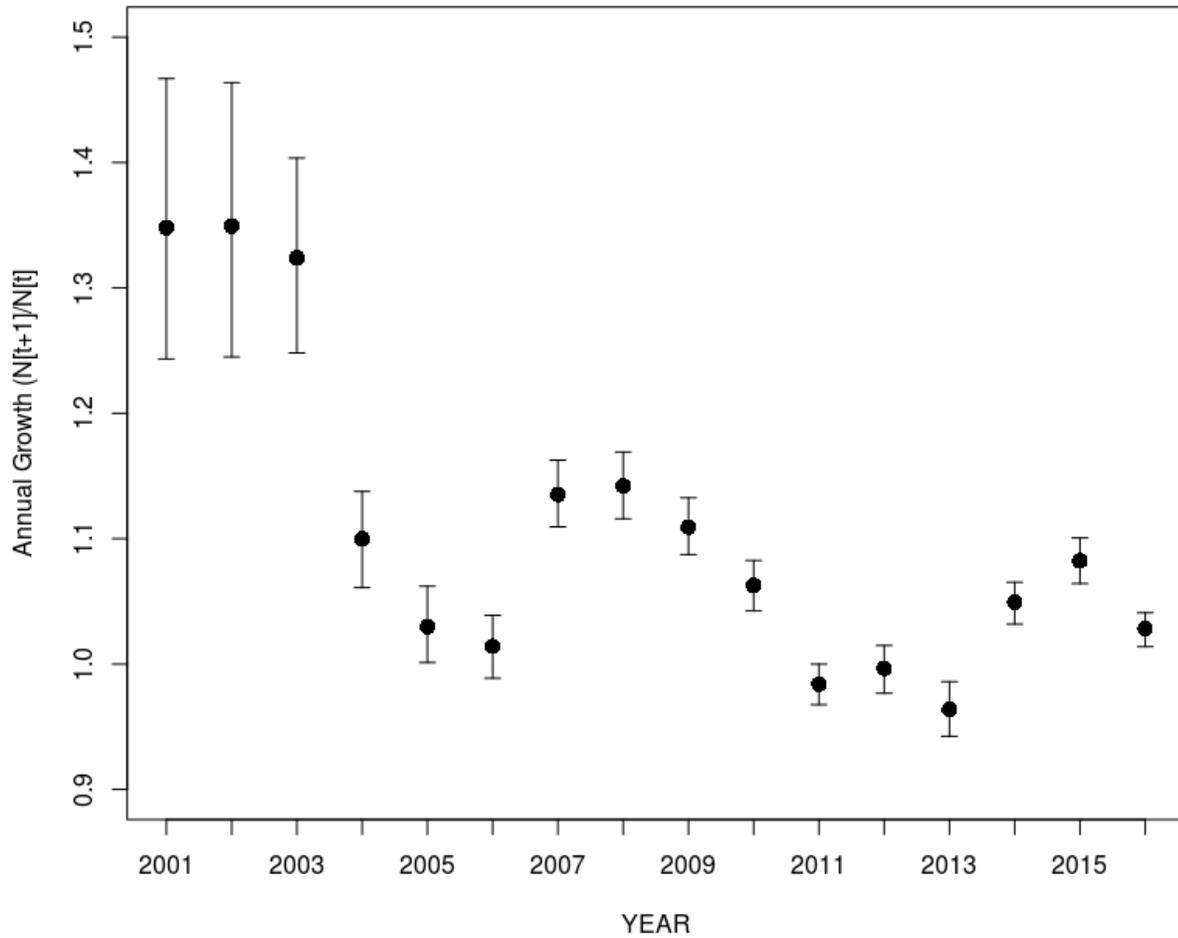
488
 489
 490

491 Figure 7. Total and sex-specific abundance of Gulf of Maine humpback whales from 2000
492 through 2016. Circles with error bars are posterior medians from a Bayesian mark-
493 recapture model allowing random fluctuation among years, age effects and adult female
494 effects on survival, as well as sex and time effects and random effects of individual
495 catchability on capture probabilities together with their 95% critical regions.



496
497
498
499

500 Figure 8: Annual estimates of population growth of the Gulf of Maine humpback whale
501 population, 2000-2014 derived from the Bayesian state-space model. Estimates for 2001-2003
502 substantially exceed the 11.8% maximum plausible rate of *in situ* annual population growth
503 (Zerbini et al. 2010).



504

505

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645

646

647

Appendix I

648 *JAGS* Code used to produce J-S state space abundance estimates

```
649 ##### Made to run in r package runjags #####
650 #-----
651 # Parameters:
652 # phi: survival probability
653 # gamma: removal entry probability
654 # p: capture probability
655 #-----
656 # States (S):
657 # 1 not yet entered
658 # 2 alive
659 # 3 dead
660 # Observations (O):
661 # 1 seen
662 # 2 not seen
663 #
664 # sex= 0 for Female, 1 for Male
665 #
666 # Full age model where intercept is for female calves, effects for age=1, age=2, age=3, all
667 others lumped (4+)
668 # Time effect on capture probability considered fixed (due to variable effective effort)
669 # Individual Catchability (Gotcha[i]) considered random  $N(0, \epsilon^2)$  in the logistic
670 # Time effect on survival ( $\eta[t]$ ) considered random  $N(0, \sigma^2)$  in the logistic
671 #
672 #-----
673
674 model {
675
676   epsilon ~ dunif(0.01, 10)      ## prior on standard deviation of catchability
677   omega<- 1/(epsilon*epsilon)    ## precision for use in jags/bugs
678
679   for (i in 1:(M))
680   {
681     Gotcha[i]~dnorm(0,omega)    ## prior on random catchability of individuals
682   }
683
684   # Priors and constraints
685   sigma~dunif(0.001,10)        ## prior for sd of random year effect on phi
686   tau<-1/(sigma*sigma)
687
688   ##### for pcap, female becomes the intercept and is the value sex at t=0 or 2000
689
690   pie~dbeta(5,5)                ## prior for sex
691   Alpha0~dunif(-5, 5)           ## Prior on Capture intercept
```

```

692 AlphaAge~dunif(-5, 5)      ## Prior on Capture juveniles
693 AlphaSex~ dunif(-5, 5)    ## Prior for intecepts rate
694 AlphaTime[1]<-0          ## Time 1 is for the dummy time interval to accomodate entry
695 AlphaTime[2]<-0          ## First Capture interval is in intercept
696 for (t in 3:(n.occasions-1)) {
697   AlphaTime[t]~dunif(-5, 5)  ## this is the fixed time effect on pcap model
698 }
699
700 # for survival parameters
701
702 for (t in 1:(n.occasions-1)){
703   gamma[t] ~ dunif(0, 1)      # Prior for entry probabilities
704 } #t
705
706 eta[1]<-0 ##### can only have entry at step 2, so ps[1,i,1,x] does not depend on phi
707 for (t in 2:(n.occasions-1)){
708   eta[t]~dnorm(0,tau)
709 } #t
710
711 b0 ~ dunif(-5,5)
712 BetaSex ~ dunif(-5, 5)      # Priors for male sex effects on survival
713 BetaAge[1] <- 0             # reference category is calves (Age=1 in input)
714 for (i in 2:6) {
715   BetaAge[i] ~ dunif(-5, 5)  # Categorical effect of each age(1,...,4+) but (Age=2,...,5 in
716 input)
717 } # i
718
719 ##### Probability models
720
721 for (i in 1:M){
722   sex[i]~dbern(pie)
723   for (t in 1:(n.occasions-1)){
724     logit(pcap[i,t])<- Alpha0 + AlphaSex*(sex[i]) + AlphaAge*(1-Adult[i,t]) + AlphaTime[t] +
725 Gotcha[i]
726     logit(phi[i,t]) <- b0 + BetaAge[Age[i,t]] + BetaSex*(1-sex[i])*Adult[i,t] + eta[t]
727   } #t for time
728 } #i for individual
729
730 # Define state-transition and observation matrices
731 for (i in 1:M){
732   # Define probabilities of state S(t+1) given S(t)
733   for (t in 1:(n.occasions-1)){
734     ps[1,i,t,1] <- 1-gamma[t]      ## Probability of no entry
735     ps[1,i,t,2] <- gamma[t]       ## Probability of entry
736     ps[1,i,t,3] <- 0              ## Must enter BEFORE death so Probability = 0
737     ps[2,i,t,1] <- 0              ## Once in stay until death
738     ps[2,i,t,2] <- phi[i,t]      ## Probability of survival

```

```

739     ps[2,i,t,3] <- 1-phi[i,t]      ## Probability of death
740     ps[3,i,t,1] <- 0              ## Dead is forever
741     ps[3,i,t,2] <- 0              ## Dead is forever
742     ps[3,i,t,3] <- 1              ## Dead is forever!
743
744     # Define probabilities of O(t) given S(t)
745     po[1,i,t,1] <- 0              ## If not entered then cannot be caught
746     po[1,i,t,2] <- 1
747     po[2,i,t,1] <- pcap[i,t]      ## If Alive this is probability of capture
748     po[2,i,t,2] <- 1-pcap[i,t]
749     po[3,i,t,1] <- 0              ## If Dead cannot be caught
750     po[3,i,t,2] <- 1
751     } #t
752 } #i
753
754     # for logistic parameters
755     for (t in 2:(n.occasions-1)){
756     pcapFA[t-1] <- 1 / (1+exp(-Alpha0 - AlphaTime[t]))      # Back-transformed recapture
757 of females
758     pcapMA[t-1] <- 1 / (1+exp(-Alpha0 - AlphaSex- AlphaTime[t]))      # Back-transformed
759 recapture of males
760     pcapFJ[t-1] <- 1 / (1+exp(-Alpha0 - AlphaAge - AlphaTime[t]))      # Back-transformed
761 recapture of juv females
762     pcapMJ[t-1] <- 1 / (1+exp(-Alpha0 - AlphaAge - AlphaSex- AlphaTime[t])) # Back-
763 transformed recapture of juv males
764     phi01[t-1] <- 1 / (1+exp(-b0-eta[t]))      # Back-transformed survival of calves
765     phi11[t-1] <- 1 / (1+exp(-b0-BetaAge[2]-eta[t]))      # Back-transformed survival of
766 yearlings
767     phi21[t-1] <- 1 / (1+exp(-b0-BetaAge[3]-eta[t]))      # Back-transformed survival of
768 2-year-olds
769     phi31[t-1] <- 1 / (1+exp(-b0-BetaAge[4]-eta[t]))      # Back-transformed survival of
770 3-year-olds
771     phi41[t-1] <- 1 / (1+exp(-b0-BetaAge[5]-eta[t]))      # Back-transformed survival of
772 3-year-olds
773     phiaf[t-1] <- 1 / (1+exp(-b0-BetaAge[6]-eta[t]))      # Back-transformed survival of
774 adult females
775     phiam[t-1] <- 1 / (1+exp(-b0-BetaSex-BetaAge[6]-eta[t]))      # Back-transformed survival
776 of adult males
777     }
778
779
780 # Likelihood
781 for (i in 1:M){
782     # Define latent state at first occasion ... in BPA this is always 1, but for HUWH we have prior
783 data about any individuals
784     z[i,1] <- 1 # Make sure that all M individuals are in state 1 at t=1
785     for (t in 2:n.occasions){

```

```

786     # State process: draw S(t) given S(t-1)
787     z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
788     # Observation process: draw O(t) given S(t)
789     y[i,t] ~ dcat(po[z[i,t], i, t-1,])
790     } #t
791   } #i
792
793   # Calculate derived population parameters
794   for (t in 1:(n.occasions-1)){
795     qgamma[t] <- 1-gamma[t]
796   }
797   cprob[1] <- gamma[1]          ##### BPA parameterization
798   for (t in 2:(n.occasions-1)){
799     cprob[t] <- gamma[t] * prod(qgamma[1:(t-1)])
800   } #t
801   psi <- sum(cprob[])          # Inclusion probability
802   for (t in 1:(n.occasions-1)){
803     b[t] <- cprob[t] / psi     # Entry probability
804   } #t
805
806   for (i in 1:M){
807     for (t in 2:n.occasions){
808       al[i,t-1] <- equals(z[i,t], 2)
809       alm[i,t-1] <- al[i,t-1]*sex[i]
810       alf[i,t-1] <- al[i,t-1]*(1-sex[i])
811     #   al[i,t-1] <- ifelse(z[i,t]=2,1,0)
812     } #t
813     for (t in 1:(n.occasions-1)){
814       d[i,t] <- equals(z[i,t]-al[i,t],0)
815     } #t
816     alive[i] <- sum(al[i,])
817   } #i
818
819   for (t in 1:(n.occasions-1)){
820     N[t] <- sum(al[,t])        # Actual population size
821     NF[t] <- sum(alf[,t])
822     NM[t] <- sum(alm[,t])
823     B[t] <- sum(d[,t])        # Number of entries
824   } #t
825   for (t in 1:(n.occasions-2)){
826     D[t] <- N[t]-N[t+1] + B[t]          ### Number dying
827   }
828   for (i in 1:M){
829     w[i] <- 1-equals(alive[i],0)
830   } #i
831   # Nsuper <- sum(w[1:M])          # Superpopulation size
832   }

```